Studies on Nematodes Parasitic on Woody Plants
1. Family Trichodoridae (Thorne, 1935) Clark, 1961*

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Five trichodorid species associated with the roots of woody plants are described and illustrated. *Trichodorus tricaulatus* n. sp. is characterized by its shape of posterior part of oesophageal bulb, which extends slightly over the intestine, three ventromedian cervical pores of the male, and the anterior half of spicules being striated. *T. aequalis* Allen, 1957, previously known only from North America, is described from central Japan. *T. longistylus* Yokoo, 1964, and *T. kurumeensis* Yokoo, 1966, are designated as junior synonyms of *T. cedarus* Yokoo, 1964, to which additional description is given. This species has a wide host range and probably is the most widespread trichodorid species in Japan. *Paratrichodorus* (*Atlantadorus*) *porosus* (Allen, 1957) was also found to parasitize a wide variety of woody plants. Variation in the number of ventromedian advulvar pores was found in several populations of this species. *P.* (*Nanidorus*) *minor* (Colbran, 1956) is less abundant in the study site but is considered native to Japan.

Attention is drawn to the intraspecific variation in three *Trichodorus* species.
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Although forests are the main terrestrial ecosystems and trees are of great importance as natural resources, the association of nematodes with forest trees is poorly known and a systematic survey of nematode fauna of this ecosystem has been rarely made.

These studies deal mainly with the systematics of parasitic nematodes of woody plants in Meiji Shrine Forest. The study site, situated in Tokyo, has an area of about 72 h*a* and consists of natural forest and afforested laurel forest. Surveys were also made in several primeval forests in central to eastern Japan for the purpose of ascertaining aboriginality of nematode species.

Methods used in this and succeeding papers are as follows; soil and root samples were collected by the author in autumn through 1975 to 1977. The specimens were extracted using Baermann's method, Christie-Perry's technique and centrifugal flotation method, killed by gentle heat, fixed in T. A. F. and processed to lactophenol containing methylene blue. Measurements were made with an ocular micrometer or with a camera lucida. Any curved organ was measured along the chord. All the drawings were made with a camera lucida.

Throughout the study Mayr's work[18] has been consulted on taxonomical problems.

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Family Trichodoridae (Thorne,1935) Clark,1961

Key to Trichodoridae females in Meiji Shrine Forest

1. Body cuticle swollen strongly, body almost straight on fixation; Ventromedian advulvar pores..... *P.(A.)porosus*(Allen,1957)
   Body cuticle not swollen so strongly, body slightly arcuate on fixation; No ventromedian advulvar pores.....2
2. Excretory pore near oesophagus base ..... *P.(N.)minor*(Colbran,1956)
   Excretory pore well anterior to oesophagus base..... 3
3. A pair of ventrosubmedian pores behind vulva; No lateral body pores ..... *T. cedarus* Yokoo,1964
   Two pairs of lateral body pores; No ventrosubmedian pores behind vulva..... 4
4. Oesophageal bulb sharply set off from intestine..... *T. aequalis* Allen,1957
   Oesophageal bulb not set off from intestine ..... *T. tricaulatus* n. sp.

Key to *Trichodorus* males in Meiji Shrine Forest

1. The first supplement at the level of the middle of retracted spicules..... *T. cedarus* Yokoo,1964
   The first supplement at the level of proximal end of spicules 2
2. Spicules not striated..... *T. aequalis* Allen, 1957
   Anterior half of spicules striated, with delicate scales ..... *T. tricaulatus* n. sp.

Trichodorus tricaulatus n.sp.
(Fig. 1.A-I)

Morphometric data: see Table 1-2.

Holotype male; L=757μm, a=25, b=5.4, T=67, stylet length=43.6μm, spicule length=43μm, gubernaculum length=15μm.

Allotype female; L=722μm, a=24, b=4.9, V=53.4, stylet length=43.1μm, G_1=17, G_2=19.

General appearance similar to other species of the genus: body cuticle not swollen so strongly, body of female slightly arcuate, and posterior end of male strongly curved ventrad on fixation. Stylet typical for the genus. Oesophageal bulb about half of oesophagus, slightly overlapping intestine ventrally. Nerve ring middle of the isthmus. Excretory pore usually at about the level of middle of the oesophagus.

Males

Three ventromedian cervical pores present in 20 specimens, two in four specimens and one in two specimens, anterior to the excretory pore and posterior to the stylet region. When three are present, the distance between the excretory pore and the first ventromedian cervical pore(EP-CP1) is lesser than CP1-CP2, and CP1-CP2 is lesser than CP2-CP3, except in one specimen where EP-CP1=7μm, CP1-CP2=3.9μm and CP2-CP3=12.3μm. When two are present, EP-CP1=7-9.4μm, and CP1-CP2=12.6-18.2μm. When only one is present, EP-CP=23.8-25μm. A pair of lateral cervical pores at about the level of nerve ring.

Three supplements almost equally spaced: the distance between them almost equal to the spicule length. Nerves of supplements enter the body anteriorly. A pair of subventral papillae just posterior to the cloaca. Caudal pores subterminal.

Testis single, outstretched. Spicules paired, similar in shape, slightly arcuate ventrally with the tip and the expanded proximal end bent; anterior half of spicules except the tip striated, delicate scales on the striated part but not discernible on the retracted spicules; the tip appears cut obliquely. Gubernaculum with curved and thickened distal end.

Females

Gonads typical for the genus, oval spermathecae with sperm. Vulval opening a minute pore. Vaginal region rounded and fig-shaped, vagina directs slightly backwards. Refractive thickening at the vulva somewhat inconspicu-

Table 1. Morphometric data on *Trichodorus tricaulatus* n. sp. (specimens from the root-zone of *Styrax japonica*)
Males (n=26)

Characters	$\bar{X}$	Range	S. D.	C	max/min
L (μm)	727	583 -827	55	0.076	1.42
Width (μm)	31	26 - 41	3.6	0.116	1.59
Neck length (μm)	139.2	117 -161	10	0.075	1.38
Stylet length (μm)	42.6	38.6- 51	2.3	0.054	1.32
Fore end to excretory pore (μm)	91	81 -115	7	0.078	1.42
Excretory pore to CP1[a,b] (μm)	4.3	2.1- 7	1.7	0.393	3.3
CP1 to CP2[b] (μm)	8.5	3.9- 10.5	1.6	0.193	2.7
CP2 to CP3[b] (μm)	12.2	8.1- 14	1.3	0.106	1.73
Spicule length (μm)	39	35 - 44	2.6	0.065	1.26
Gubernaculum length (μm)	16	11 - 19	2.5	0.158	1.70
Cloaca to SP1[c] (μm)	37	32 - 43	2.8	0.075	1.31
SP1 to SP2 (μm)	36	29 - 46	3.6	0.099	1.58
SP2 to SP3 (μm)	39	29 - 49	4.4	0.112	1.69
Testis length (μm)	467	355 -576	50	0.107	1.62
Ratios-a	23	19 - 26	2.3	0.097	1.40
-b	5.2	4.2- 5.8	0.4	0.081	1.38
-T	64	55 - 70	3.8	0.059	1.27
-Fore end to excretory pore/Neck length (%)	66	55 - 91	7.3	0.110	1.66

[a] First cervical pore. [b] Data on specimens with three ventromedian cevical pores (n=20).
[c] First supplement.

Table 2. Morphometric data on *Trichodorus tricaulatus* n. sp. (specimens from the root-zone of *Styrax japonica*)
Females (n=14)

Characters	$\bar{X}$	Range	S. D.	C	max/min
L (μm)	709	602 -785	53	0.075	1.31
Width (μm)	32	25 - 34	2.6	0.082	1.36
Neck length (μm)	135	119 -148	8	0.060	1.24
Stylet length (μm)	42.2	38.6- 44	1.7	0.041	1.14
Fore end to excretory pore (μm)	88	77 - 95	5	0.062	1.25
Fore end to vulva (μm)	384	327 -427	28	0.074	1.30
Ant. ovary length (μm)	136	117 -155	13	0.093	1.32
Post. ovary length (μm)	138	104 -164	15	0.106	1.57
Vulva to ant. lateral body pore (μm)	116	99 -130	9	0.081	1.31
Vulva to post. lateral body pore (μm)	18	13 - 24	3.3	0.176	1.89
Ratios-a	23	18 - 26	2.5	0.109	1.34
-b	5.3	4.6- 6.2	0.5	0.089	1.35
-V	54.1	52 - 56	1.2	0.023	1.09
$-G_1$	19	17 - 22	1.9	0.099	1.3
$-G_2$	19	15 - 22	2.0	0.104	1.47
-Fore end to excretory pore/Neck length (%)	67	58 - 85	6.7	0.101	1.48

ous, triangular in lateral view.

Two pairs of lateral body pores present; the anterior pair situated about the middle between the oesophagus base and the vulva, the posterior pair half to one body-width behind the vulva.

Anus subterminal. Caudal pores subterminal.

One specimen has prominent ventromedian cervical pores anterior to the excretory pore; EP-CP1=6.3μm, CP1-CP2=16.8μm, possessing no lateral cervical pores. In other respects this specimen has normal female morphology; two

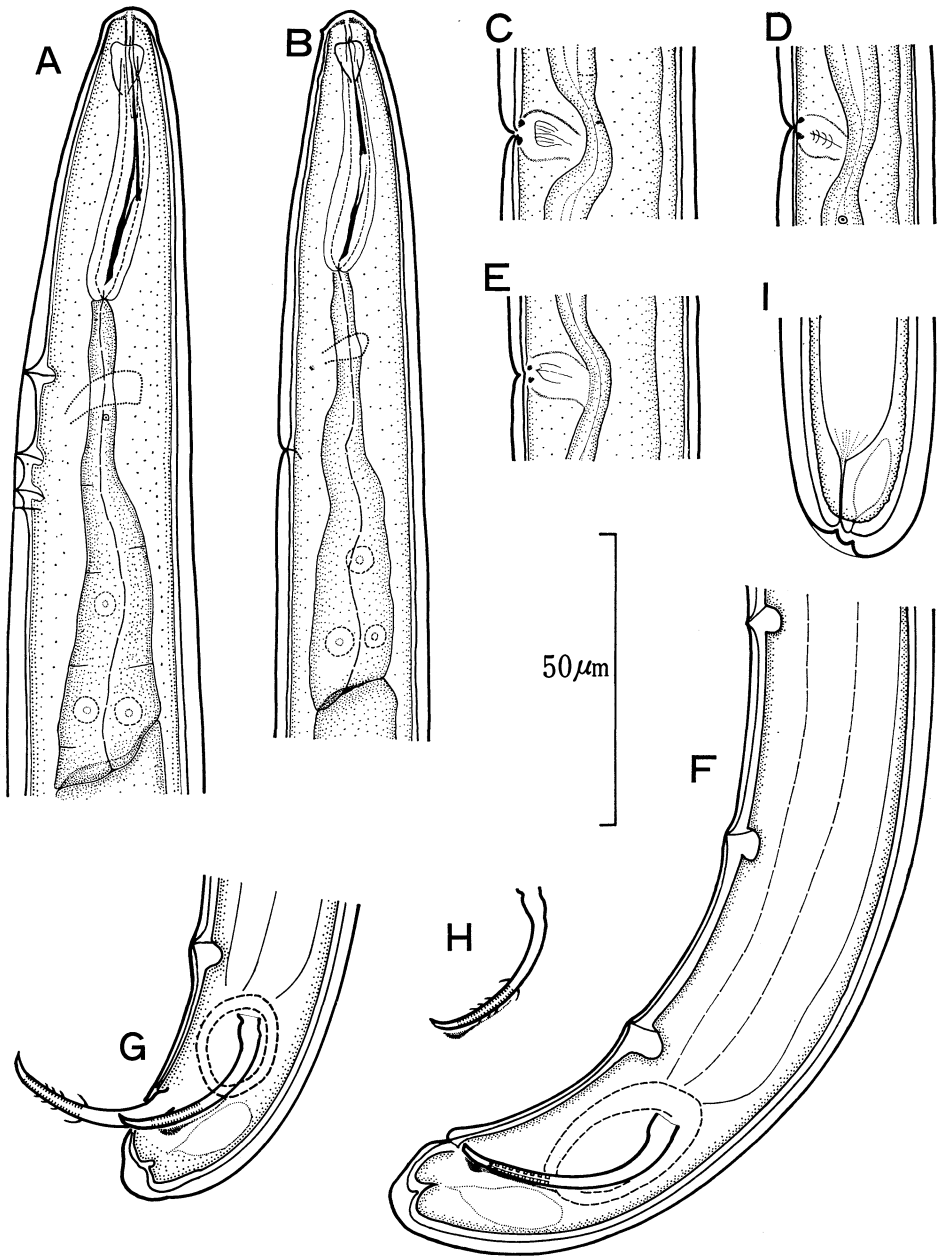

Fig. 1. *Trichodorus tricaulatus* n. sp. A: Neck region of male. B: Neck region of female. C-E: Vulval region. F: Posterior end of male. G: Posterior end of male showing protruded spicule. H: Spicule and gubernaculum. I: Posterior end of female.

pairs of lateral body pores present, $G_1=15$, $G_2=20$.

Juveniles

Out of 19 juveniles, 16 have developing gonads discernible at low magnification. Measurements of these specimens are as follws;

L=526(463-662)μm, a=21(14-24), b=4.3(3.8-5), stylet length=38.6(35-42)μm, gonad length=40

(24–56)μm, gonad length/L (%)=7.6(4.4–10.7).

General appearance similar to females. Oesophageal bulb slightly extends over the intestine ventrally and laterally. Excretory pore at the level of middle of the oesophagus. A pair of caudal pores subterminal. Anus subterminal.

Type specimens

Holotype; Male collected on October 30, 1976; slide no. *Trichodorus* 2–10; kept in Laboratory of Forest Zoology Nematode Collection, Faculty of Agriculture, University of Tokyo, Tokyo, Japan.

Allotype; Female; slide no. *Trichodorus* 2–13; other data as for holotype.

Paratypes; 25 males, 13 females and 19 juveniles; data as for holotype.

Type habitat and locality

Soil around the roots of *Styrax japonica*, Meiji Shrine Forest, Tokyo, Japan.

Host species and distribution

This species has been collected around the roots of the following plant species by the author in Meiji Shrine Forest; *Quercus acutissima, Q. serrata, Neolitsea sericea, Ilex crenata, Cleyera japonica, Styrax japonica, Sambucus racemosa.* Since these species are all of natural growth, *T. tricaulatus* n. sp. is considered native to this site, accordingly to Japan.

Diagnosis and relationship

T. tricaulatus n. sp. is characterized by the oesophagus overlapping the intestine ventrally; male with three ventromedian cervical pores, the first supplement slightly anterior to the proximal end of spicules, characteristic spicule shape, anterior half of spicules striated, delicate scales on the striated part of spicules.

Other species of *Trichodorus* with oesophagus ventrally overlapping intestine are *T. cylindricus*[8], *T. viruliferus*[9], *T. velatus*[10] and *T. variopapillatus*[10]; *T. tricaulatus* n. sp. male differs from them in arrangement of ventromedian cervical pores, of which one is situated in the stylet region in the four species, and also in the shape of the spicule. *T. tricaulatus* n. sp. female differs from them in the vaginal shape.

T. tricaulatus n. sp. appears closest to *T. aequalis*[1,14] and *T. sparsus*[14,30] in the shape of spicules and gubernaculum, arrangement of supplements of the male, arrangement of lateral body pores, and the vaginal shape of the female. The male of *T. tricaulatus* n. sp. differs from the two species in the distribution of the striation of spicules and in the number of ventromedian cervical pores; i. e., in *T. aequalis* spicules have no striation nor scales, in *T. sparsus* both occur throughout spicules except the tip and the proximal end, both species have only two ventromedian cervical pores. The female of *T. tricaulatus* n. sp. cannot be distinguished from those two species by the vaginal shape nor by the distribution of lateral body pores, but differs only in the shape of oesophageal bulb, i. e., both species have oesophagus set off from the intestine.

T. tricaulatus n. sp. male and female key out to *T. sparsus* in Esser's key[6], male keys out to *T. pakistanensis* in Siddiqi's key[26], and female keys out to *aequalis* + *sparsus* in Loof's key[15]. The male of this species is distinguished from that of *T. pakistanensis* by its shorter body, the shape of spicules, the shape of oesophageal bulb, or by the arrangement of supplements.

In addition to the above-mentioned resemblance to *T. aequalis* and *T. sparsus*, wrinkles of the inner cuticle noted by Loof[14] have been observed in several specimens of *T. tricaulatus* n. sp., although taxonomical value of this character is not clear.

Variability of some characters

Quantitative characters

The variability of each character is expressed as coefficient of variation in Table 1–2. Stylet length of both sexes and spicule length showed the least variability. Gubernaculum length appears the most variable, body length and neck length less variable, and body width and length of both ovaries intermediate. Rates

of the maximum to the minimum of stylet length and of spicule length were found the least, and they appear the most stable characters of all the morphological measurements. Variability of testis length was found greater than that of body length.

Of ratios V value is by far the least variable. Other ratios such as a, b, T, G_1, G_2 and fore end to excretory pore/neck length showed greater variability.

Qualitative characters

The shape of the posterior part of oesophagus, the shape of spicules and the shape of gubernaculum are very stable and can be used for diagnoses of this species. The shape of vaginal region is also an important diagnostic character.

As already mentioned three supplements are almost equally spaced and the distance among them are almost equal to spicule length. Both coefficient of variation and max/min show that the distance between the cloaca and the first supplement (Clo–SP1) is the least variable, SP2–SP3 the most, and SP1–SP2 intermediate, so that the location of the first supplement in relation to the spicules is another diagnostic character.

The distance CP2–CP3, CP1–CP2 and EP–CP1 have been already described. CP2–CP3 is usually greater than CP1–CP2, and CP1–CP2 than EP–CP1. This character appears very stable. Both coefficient of variation and max/min are the greatest for EP–CP1, the smallest for CP2–CP3, and intermediate for CP1–CP2.

As to the lateral body pores of the female, the location of the posterior pair in relation to the vulva is very variable relatively to that of the anterior one.

Meristic characters

The number of ventromedian cervical pores was found very variable in this species, although the significance is not known.

The number of lateral body pores in female is stable.

Although Loof[14,15] states that supplemnt number is much more variable in so-called *T. aequalis*-group than in other *Trichodorus* species, this species, closest to the former group, has three supplements in every male of 35 specimens examined.

Trichodorus aequalis Allen, 1957
(Fig. 2. A–I)

Nine males, 20 females and 10 juveniles of *Trichodorus aequalis* were collected from the root-zone of *Rhododendron obtusum* and examined for study. Measurements and detailed morphology well correspond with Allen's description[1] and that of Loof[14] except for the stylet length. *Morphometric data*: see Table 3–4.

Males

The specimens from *Rhododendron obtusum* differ from the type material[1,14] in the following characters; stylet shorter (41.4–47.5μm vs. 47–59 μm), body more slender (a=19–25 vs. 17–20) in *Rhododendron* specimens. Although both dimensions may vary through fixation, shrinkage of stylet was not observed in these specimens.

Clo-SP1 the least and slightly lesser than spicule length, so that SP1 located at level of proximal end of spicules. SP2–SP3 the greatest and almost equal to spicule length.

CP1–CP2 always greater than EP–CP1, the ratio CP1–CP2/EP–CP1=2.3 in mean.

Females

Females from *Rhododendron* also differ from the type material in shorter stylet length; 42.3–48μm vs. 50–74μm.

Vaginal shape somewhat variable (Fig.2.C–E) but similar in general feature, shape of refractive thickening at vulva stable.

Excretory pore in both sexes located at 77% neck length from fore end in mean.

Juveniles

Genaral appearance similar to females except for tail shape; tail somewhat acute in several specimens (Fig.2.H–I). Wrinkles of the inner

Table 3. Morphometric data on *Trichodorus aequalis*
Males (n=9)

Characters	$\bar{X}$	Range	S. D.	C	max/min
L (μm)	676	620 -750	42	0.063	1.21
Width (μm)	31	25 - 34	2.5	0.081	1.36
Neck length (μm)	127.5	117 -140	10	0.080	1.18
Stylet length (μm)	44.6	41.4- 47.5	1.5	0.034	1.15
Fore end to excretory pore (μm)	101	91 -112	6.0	0.059	1.23
Excretory pore to CP1 (μm)	9.6	4.9- 16.1	3.0	0.311	3.29
CP1 to CP2 (μm)	20.2	14 - 24.2	2.7	0.134	1.73
Spicule length (μm)	40	38 - 40.5	0.7	0.017	1.06
Gubernaculum length (μm)	16	12 - 18	2.0	0.126	1.50
Cloaca to SP1 (μm)	33	32 - 37	1.5	0.045	1.17
SP1 to SP2 (μm)	35	30 - 40	3.4	0.097	1.33
SP2 to SP3 (μm)	40	32 - 46	4.6	0.116	1.42
Testis length (μm)	419	370 -471	41	0.098	1.27
Ratios-a	22	19 - 25	1.7	0.079	1.28
-b	5.4	4.5- 6.6	0.7	0.122	1.47
-T	62	58 - 69	3.6	0.059	1.18
-CP1-CP2/EP-CP1	2.3	1.3- 3.9	0.8	0.340	3.0
-Fore end to excretory pore/Neck length (%)	77	69 - 85	5.5	0.071	1.22

Table 4. Morphometric data on *Trichodorus aequalis*
Females (n=20)

Characters	$\bar{X}$	Range	S. D.	C	max/min
L (μm)	708	601 -821	53	0.075	1.37
Width (μm)	36	32 - 43	3.2	0.089	1.34
Neck length (μm)	124	104 -143	11	0.089	1.37
Stylet length (μm)	45	42.3- 48	1.5	0.033	1.13
Fore end to excretory pore (μm)	100	80 -111	7	0.075	1.38
Fore end to vulva (μm)	380	333 -427	28	0.074	1.28
Ant. ovary length (μm)	147	94 -185	24	0.165	1.97
Post. ovary length (μm)	161	131 -196	21	0.129	1.49
Vulva to ant. lateral body pore (μm)	93	62 -108	14	0.156	1.73
Vulva to post. lateral body pore (μm)	26	13 - 42	10.1	0.382	3.33
Ratios-a	20	18 - 22	1.5	0.074	1.27
-b	5.8	4.5- 6.8	0.7	0.121	1.51
-V	53.6	50.7- 56.1	1.5	0.027	1.08
$-G_1$	21	16 - 27	2.7	0.130	1.74
$-G_2$	23	20 - 27	2.3	0.100	1.39
-Fore end to excretory pore/Neck length (%)	77	54 - 93	10.1	0.131	1.72

Juveniles (n=10) : L=515(444-627)μm, a=18(16-21), b=4.8(3.6-6.2), stylet length=41(38.7-44)μm, gonad length=40(25-70)μm, Gonad length/L (%)=7.6(5.6-11.4).

cuticle mentioned by Loof[14] were observed in most males, females and juveniles.

Variability of some characters

The variable tendency of some characters is generally similar to that of *T. tricaulatus* n.sp.; spicule length, V value and stylet length have the least variability, all the qualitative characters mentioned for *T. tricaulatus* n. sp. appear quite stable except for the vaginal shape which is somewhat variable.

Variation in the number of ventromedian cervical pores has not been found in the specimens from *Rhododendron* soil. As with *T. tricaulatus* n. sp., EP-CP1 appears more variable

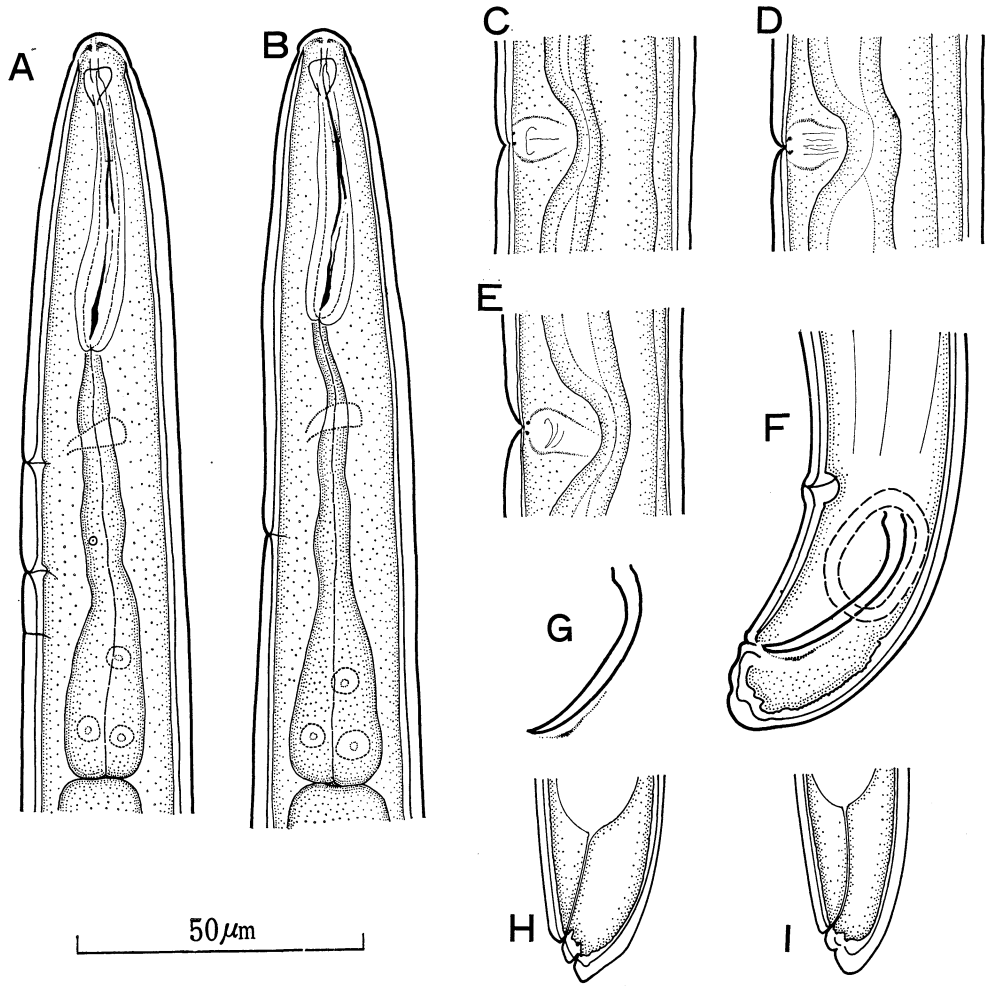

Fig. 2. *Trichodorus aequalis*, Allen. A: Neck region of male. B: Neck region of female. C-E: Vulval region. F: Posterior end of male. G: Spicule and gubernaculum. H-I: Posterior end of juveniles.

and CP1–CP2 less variable.

As to the distribution of ventromedian cervical pores it is noted that both EP–CP1, CP1–CP2 and the ratio CP1–CP2/EP–CP1 correspond with those of type material by Loof[14] (EP–CP1 =Loof's P2–EP, and CP1–CP2=P1−P2).

Variation of supplement number has not been observed in Japanese specimens.

T. aequalis has been reported associated with several woody plants in the United States,[1,27,28] although the distribution is quite restricted in USA. Sturhan[29] and Rössner[22] reported this species from Germany, although the European population has been referred to *T. sparsus* Szczygiel, 1968 by Wyss.[32]

According to Loof,[14] Alphey and Boag[2] and Heath et al.,[7] *T. sparsus* has been found throughout Europe, and in a forest nursery in Great Britain this species is considered introduced with imported plant materials or soil, and *T. hooperi* Loof, 1973, the third species of the so-called *aequalis*-group, has been recorded only from a few sites of Great Britain. Since *T. tri-*

Table 5. Morphometric data on different populations of *Trichodorus cedarus*
Males

	Cornus controversa n=23				
Characters	$\bar{X}$	Range	S. D.	C	max/min
L (μm)	603	530 -688	40	0.066	1.3
Width (μm)	34	31 - 42	2.8	0.080	1.38
Neck length (μm)	137	121 -160	9.2	0.067	1.33
Stylet length (μm)	55.8	51.4- 63	2.9	0.051	1.23
Fore end to excretory pore (μm)	104	97 -112	4	0.037	1.15
Excretory pore to CP1 (μm)	7.4	3.2- 10.5	1.8	0.243	3.28
CP1 to CP2 (μm)	7.5	4.9- 9.1	1.1	0.146	1.86
CP2 to CP3 (μm)	10.2	5.6- 14.7	1.8	0.181	2.6
Spicule length (μm)	40	36 - 43	1.7	0·041	1.18
Gubernaculum length (μm)	20	18 - 21	1.0	0.05	1.2
Cloaca to SP1 (μm)	23	22 - 26	1.2	0.053	1.21
SP1 to SP2 (μm)	30	23 - 34	2.9	0.095	1.46
SP2 to SP3 (μm)	36	18 - 45	6.6	0.192	2.5
Testis length (μm)	393	273 -433	39	0.098	1.59
Ratios-a	18	15 - 20	1.3	0.076	1.32
-b	4.4	3.9- 4.9	0.3	0.067	1.26
-T	65	51 - 74	4.2	0.065	1.45
-Fore end to excretory pore/Neck length (%)	76	67 - 86	5.5	0.072	1.29

Table 6. Morphometric data on different populations of *Trichodorus cedarus*
Females

	Cornus controversa n=31				
Characters	$\bar{X}$	Range	S. D.	C	max/min
L (μm)	575	501 -670	36	0.063	1.34
Width (μm)	34	29 - 40	2.4	0.071	1.38
Neck length (μm)	130	113 -157	9.3	0.072	1.39
Stylet length (μm)	56.2	51 - 61.1	2.7	0.048	1.198
Fore end to excretory pore (μm)	102	90 -107	4	0.042	1.19
Fore end to vulva (μm)	335	303 -385	18	0.054	1.27
Ant. ovary length (μm)	135	108 -171	15	0.114	1.58
Post. ovary length (μm)	119	90 -157	16	0.132	1.74
Vulva to ventrosubmedian pore (μm)	14	4.2- 23.8	3.9	0.279	5.67
Ratios-a	17	15 - 19	1.0	0.056	1.29
-b	4.5	3.6- 5.3	0.4	0.085	1.47
-V	58.3	56 - 61.1	1.5	0.026··	1.09
-G_1	23	18 - 29	2.7	0.115	1.63
-G_2	21	16 - 25	2.3	0.112	1.59
-Fore end to excretory pore/Neck length (%)	79	63 - 93	5.7	0.072	1.46

caulatus n. sp. is regarded as belonging to *T. aequalis*-group, two species of this group occur sympatrically in Japan, although it is not known whether *T. aequalis* is native to Japan.

Trichodorus cedarus Yokoo, 1964
(Fig.3. A–I)
=*Trichodorus longistylus* Yokoo, 1964, new synonymy
=*Trichodorus kurumeensis* Yokoo, 1966, new synonymy

Quercus acutissima n=25		*Neolitsea sericea* n=19		*Kerria japonica* n=58	
$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range
554	(433 -712)	599	(496 -715)	600	(525 -697)
31	(25 - 36)	32	(28 - 36)	35	(29 - 40)
122	(104 -157)	135	(119 -151)	129	(107 -146)
51	(41 - 58)	54	(43 - 57)	57	(52 - 61)
89	(65 -113)	97	(90 -106)	99	(88 -115)
6.4	(2.2- 10.2)	7.8	(5.3- 11.9)	7.4	(2.8- 14.7)
6.2	(4.2- 8.4)	8.0	(6 - 10.5)	8.1	(5.6- 16.1)
7.9	(3.6- 10.8)	10.7	(8.1- 13.3)	10.7	(6 - 15.4)
38	(35 - 43)	41	(35 - 46)	42	(38 - 53)
17	(14 - 21)	19	(17 - 21)	20	(19 - 24)
22	(20 - 26)	22	(14 - 23)	23	(14 - 36)
27	(20 - 34)	29	(20 - 32)	30	(17 - 39)
31	(22 - 40)	38	(27 - 44)	38	(22 - 52)
337	(259 -440)	373	(292 -473)	399	(316 -484)
18	(12 - 22)	19	(17 - 22)	17	(15 - 23)
4.6	(3.7- 5.5)	4.4	(3.7- 5.1)	4.6	(3.9- 5.3)
62	(52 - 72)	65	(61 - 71)	67	(57 - 81)
74	(56 - 82)	73	(65 - 80)	77	(65 - 89)

Quercus acutissima n=31		*Neolitsea sericea* n=22		*Kerria japonica* n=67	
$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range
603	(460 -788)	571	(519 -673)	586	(494 -651)
32	(25 - 46)	33	(28 - 36)	36	(30 - 42)
113	(87 -137)	129	(119 -140)	127	(105 -149)
51	(45 - 58)	55	(50 - 60)	57	(52 - 64)
86	(72 -106)	96	(86 -107)	99	(81 -114)
307	(245 -463)	311	(231 -360)	333	(284 -364)
130	(72 -146)	140	(109 -182)	140	(105 -166)
120	(92 -155)	134	(110 -166)	135	(109 -172)
12	(4.9- 18.6)	12	(4.9- 16.1)	15	(9.8- 24.5)
19	(12 - 26)	17	(15 - 20)	16	(15 - 19)
5.3	(4.5- 7.4)	4.4	(3.7- 5.5)	4.6	(3.9- 5.6)
56.4	(53.5- 59.4)	57.2	(55 - 60.3)	56.9	(53.3- 60.3)
22	(13 - 28)	25	(20 - 30)	24	(18 - 28)
20	(15 - 27)	23	(19 - 28)	23	(18 - 28)
77	(65 - 86)	74	(68 - 88)	77	(67 - 88)

T. cedarus, originally described by Yokoo in 1964[33] from poorly fixed specimens, was redescribed and redefined by Mamiya in 1967.[17] When Mamiya redescribed *T. cedarus*, three closely related species had been described by Yokoo, i. e., *T. longistylus* Yokoo, 1964. *T. cedarus* Yokoo, 1964, and *T. kurumeensis* Yokoo, 1966.[34] Mamiya identified his specimens as *T. cedarus* on the basis of stylet length and morphology of ovaries. The publication of a description of *T. kurumeensis* was behind the time of Mamiya's work.

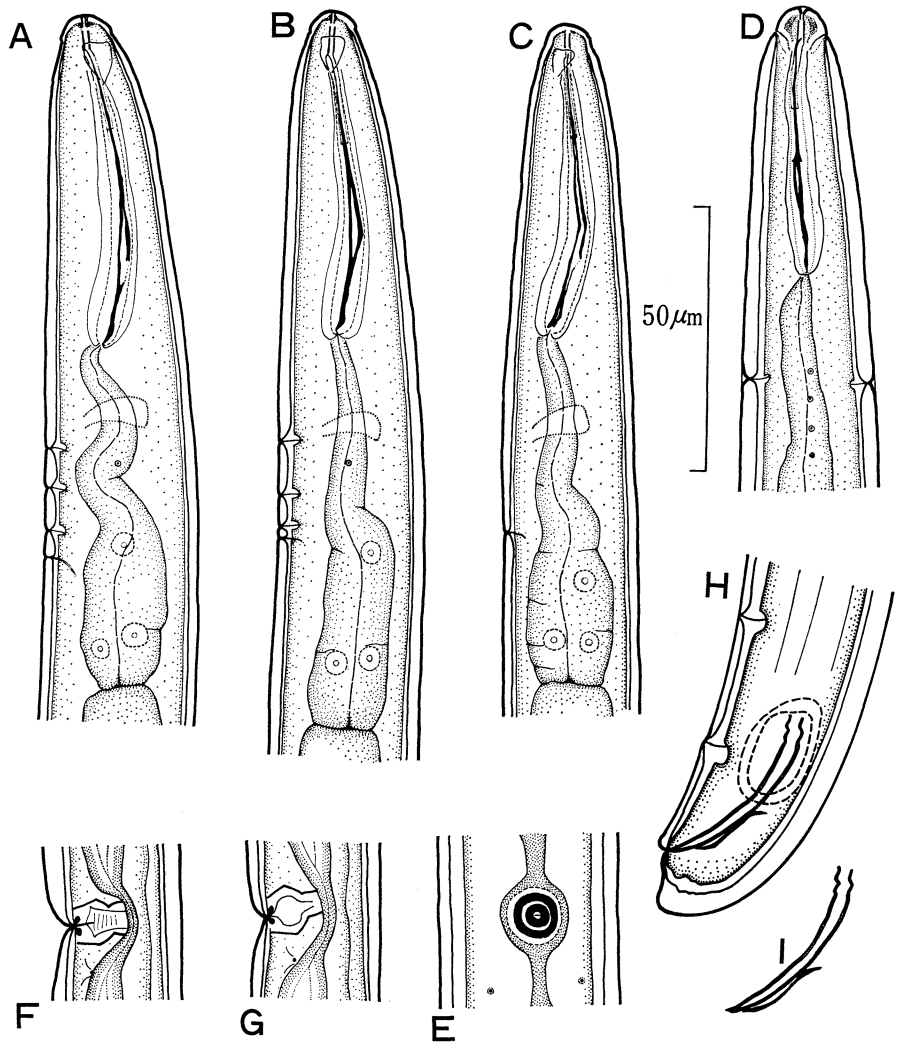

Fig. 3. *Trichodorus cedarus*, Yokoo. A-B: Neck region of males. C: Neck region of female. D: Anterior end of male, ventral view. E: Vulval region, ventral view. F-G: Vulval region. H: Posterior end of male. I: Spicule and gubernaculum.

Some differences in morphology appeared between the author's observation and that described by Mamiya.

Morphometric data: see Table 5-6.

Morphological description emended

Males

A pair of lateral cervical pores located at level of the third ventromedian cervical pore; spicule slightly curved ventrally, the tip appears cut obliquely, usually without scales but in one specimen delicate scales observed on the middle part of protruded spicule; supplements usually three, but two males out of 263 with four supplements; number of ventromedian cervical pores rather variable (Table 7).

Females

Lateral body pores absent; a pair of ventrosubmedian pores one-sixth to half body-width posterior to the level of vulva.

Although Mamiya[17] denied the original desc-

ription and redescribed *T. cedarus* males as not having lateral cervical pores, a pair of lateral cervical pores do exist on all the specimens examined as described on other *Trichodorus* species. Lateral body pores of females were not mentioned by Yokoo nor by Mamiya. So far as known *T. cedarus* is the only *Trichodorus* species without lateral body pores, though several species have the posterior pair only.[1,4,8,9,10,14,21,23,24,26] It is likely that the ventrosubmedian pore is homologous to the posterior lateral body pore.

Table 7. Variation in the number of ventromedian cervical pores in males of *Trichodorus cedarus*

Host species[a]	n	Number of ventromedian cervical pores 4	3	2	1
Torreya nucifera	5		5		
Pinus thunbergii	2		2		
P. densiflora	1		1		
Cryptomeria japonica	4		3	1	
Chamaecyparis obtusa	6		6		
Carpinus tschonoskii	2		2		
Quercus acutissima	28		27		1
Castanea crenata	1		1		
Castanopsis cuspidata	1		1		
Zelkova serrata	38	1	37		
Celtis sinensis	7		7		
Cercidiphyllum japonicum	8		8		
Magnolia obovata	4		4		
Cinnamomum camphora	2		2		
Neolitsea sericea	19		17	2	
Kerria japonica	58		55	2	1
Prunus yedoensis	16		16		
Daphniphyllum macropodum	8		8		
Rhus succedanea	2		2		
Camellia sinensis	4		4		
C. japonica	1		1		
Eurya japonica	4		4		
Fatsia japonica	7		7		
Cornus controversa	23		22	1	
Rhododendron indicum[b]	6		4	2	
Callicarpa japonica	6		6		
Total	263	1	252	8	2

[a] Males not obtained from: *Quercus phillyraeoides*, *Q. myrsinaefollia*, *Viburnum awabuki*.
[b] In the garden of Univ. Tokyo.

Relationships of Yokoo's related species

In describing *T. cedarus*, Yokoo[33] recognized its resemblance to *T. longistylus*. *T. kurumeensis*[34] also resembles to *T. longistylus* and *T. cedarus*. Yokoo[34] regarded them as separate species because of differences in morphological characters as shown in Table 8.

Because of the fact that type specimens of these species are all lost, we have no other way than examining the descriptions by Yokoo and their type localities to study more their relationships.

As was pointed out by Mamiya,[17] nematode specimens used for descriptions of *T. longistylus* and *T. cedarus* by Yokoo apppear to be shrunken through fixation. Figures and photographs for a description of *T. kurumeensis* by Yokoo show that specimens were apparently shrunken, too. It is very likely that the location of the third ventromedian cervical pore (CP3) of *T. longistylus* and *T. cedarus* is due to poor fixation and that the arrangement of ventromedian cervical pores in relation to the stylet is quite the same for the three species.

Yokoo[34] also states that the distribution of supplements differs between *T. kurumeensis* and the other two species, but he used only two males for a description of *T. kurumeensis* suggesting the posterior part of specimens in Fig.1-5,7 strongly shrunken through fixation. Fig.1-7 of Yokoo[34] shows clearly that *T. kurumeensis* male had the same distribution of supplements as *T. longistylus* and *T. cedarus*.

Table 8. The distinction between the three species described by Yokoo (based on Yokoo, 1964 and 1966)

	T. longistylus	*T. cedarus*	*T. kurumeensis*
Stylet length (μm)	72.5-75	58.5-62.5	47.5-54
Location of CP3	within stylet range	within stylet range	behind stylet
Ovaries	outstretched	reflexed	the posterior reflexed, the anterior outstretched

It has been increasingly clear that the shape of refractive thickening at the vulva and the shape of spicules are among the most important characters to the systematics of trichodorids.[11,15,26] Although none of detailed morphology of refractive thickening for the three species was described or illustrated by Yokoo, spicules were illustrated in detail. His figures and photographs show that the shape of spicules and gubernaculum appear so close in the three species that they cannot be distinguished.

As to the stylet length of *T. cedarus*, the author found that this character is so variable in this species(41–65μm in Meiji Shrine populations) and of less value for species separation. Yokoo's figures show the length of stylet as approximately 64μm for *T. cedarus* and 68μm for *T. longistylus*, but are given in his descriptions, 58.5–62.5μm and 72.5–75μm, respectively. Difference in the stylet length between *T. longistylus* given by Yokoo and *T. cedarus* from Meiji Shrine is not small, but, since *T. cedarus* has a very variable stylet length, it is unreasonable to separate longer stylet populations and shorter stylet populations into two species.

The only distinction between *T. longistylus*, *cedarus* and *kurumeensis* is the morphology of ovaries. But according to Coomans, Geraert and Decraemer (Pers. Comm.), all the dorylaimids have reflexed ovaries, and it is probably the same with *T. longistylus* and *T. kurumeensis*.

In addition, Mamiya obtained *Trichodorus* specimens from the type locality of *T. longistylus* and identified them as *T. cedarus*(Pers. Comm.). Therefore there is no doubt that the three species are conspecific.

T. longistylus has page precedence, but *T. cedarus* is better defined.[17] Accordingly *T. cedarus* is selected as the name of this taxon by the action of the first reviser, and *T. longistylus* and *T. kurumeensis* are put in the junior synonyms of *T. cedarus*.

Host species and distribution

T. cedarus had been found associated with various species of conifers at forest nurseries almost all over Japan.[12,17,35] Surveys in Meiji Shrine Forest revealed that this species is also associated with various forest trees; five species of conifers and 23 species of broad-leaved trees(Table 7). It is supposed that this species is of wide distribution on a wide variety of plant species in Japan.

Lee[13] reported this species from South Korea associated with soybean, cabbage, apple and barley. This is the first record for this species outside Japan. Measurements given by Lee correspond with those given by Yokoo,[33] and Mamiya[17] and in this paper. Since description given by Lee includes no detailed description or illustration on the morphology of spicules and gubernaculum, the shape of vagina, and body pores of females, the Korean population cannot be exactly identified.

Variability of some characters(based on a population from *Cornus controversa*)

Spicule length, gubernaculum length, and stylet length of both sexes showed the least variability. Length of ovary is regarded the most variable. As shown in table, stylet length is variable among the populations.

Of ratios, V value is by far the least variable, and G_1 and G_2 are the most. Fore end to excretory pore/neck length is not so variable as with *T. tricaulatus* n. sp. and *T. aequalis*.

Qualitative characters such as the shape of spicule, gubernaculum, vagina, and the distribution of supplements in relation to the spicules appear very stable. The location of the excretory pore in relation to the neck region is rather stable unlike those with *T. tricaulatus* n. sp. and *T. aequalis*. As to the location of ventrosubmedian pores expressed as "vulva to ventrosubmedian pore", it is as much variable as those of the posterior lateral body pores in *T. tricaulatus* n. sp. and *T. aequalis*. Since two ventrosubmedian pores are usually at different distances from the vulva, the location is not dependent on body width.

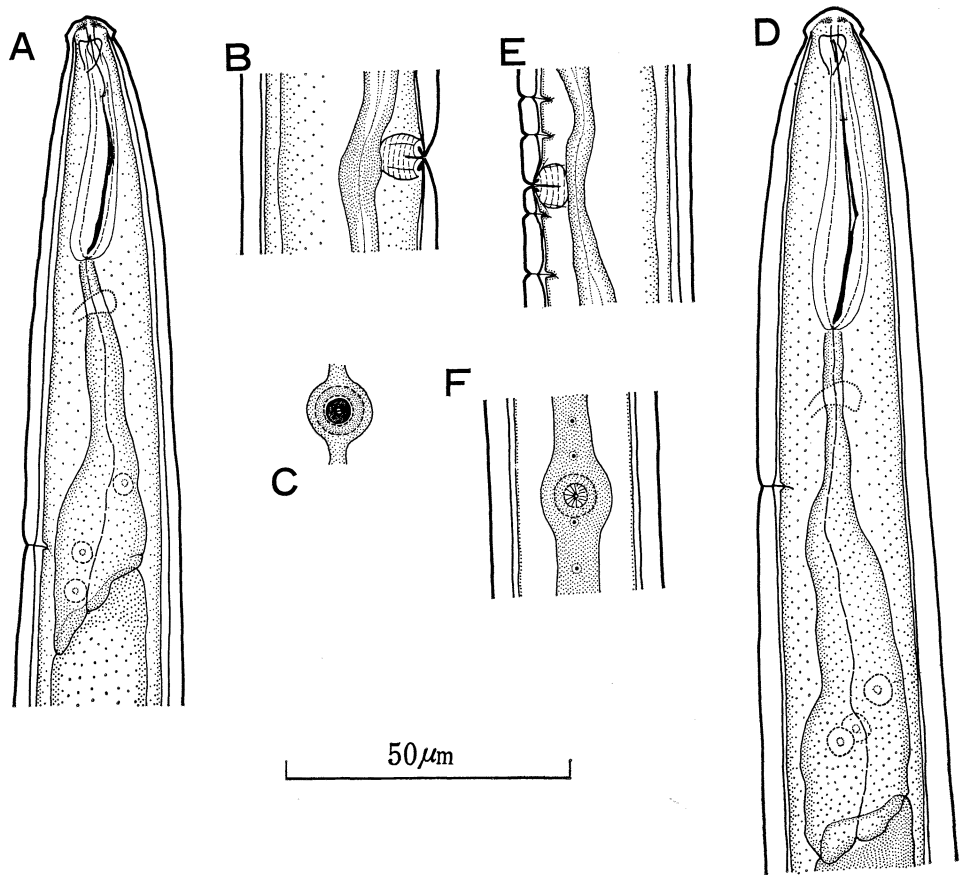

Fig. 4. *Paratrichodorus* (*Nanidorus*) *minor* (Colbran) : A-C. A: Neck region of female. B: Vulval region. C: Vulval region, ventral view. *Paratrichodorus* (*Atlantadorus*) *porosus* (Allen) : D-F. D: Neck region of female. E: Vulval region. F:Vulval region, ventral view.

The presence or absence of scales on the spicule is considered a very stable character, which was found in one specimen of *T. cedarus*. Scales on the spicule of trichodorids are membranous structure,[20] and when they adhere to the surface of the spicule, they probaly cannot be observed with an optical microscope. Study on the ultrastructure by SEM is needed for the clarification of the nature of scales on the spicule of *T. cedarus*.

The number of ventromedian cervical pores and supplement number are variable in this species (Table 7). According to Loof,[14,15] supplement number is very constant except in the *T. aequalis*-group. Further study is needed as to the nature of supplement number.

As with *T. tricaulatus* n. sp. and *T. aequalis*, EP-CP1 is the most variable. In summary for three *Trichodorus* species found in Japan, Clo-SP1 is the least variable, the location of SP1 in relation to the spicule is stable, and EP-CP1 is the most variable.

Paratrichodorus (*Nanidorus*) *minor* (Colbran, 1956) Siddiqi, 1974

(Fig. 4.A-C)

=*Trichodorus minor* Colbran, 1956

=*Trichodorus christiei* Allen, 1957

Table 9. Morphometric data on *Paratrichodorus* (*N.*) *minor* (specimens from the root-zone roots of *Quercus serrata*)
Females (n=6)

Characters	$\bar{X}$	Range
L (μm)	634	482 -783
Width (μm)	38	24 - 47
Neck length (μm)	123	91 -142
Stylet length (μm)	36	33 - 40
Fore end to excretory pore(μm)	104	89 -123
Fore end to vulva (μm)	339	279 -371
Ant. ovary length (μm)	166	106 -194
Post. ovary length (μm)	156	42 -192
Ratios-a	17	15 - 21
-b	4.8	4.9- 5.3
-V	53.5	51.3- 53
-G_1	25	22 - 28
-G_2	22	9 - 27
-Fore end to excretory pore/Neck length (%)	95	87 - 98

=*Paratrichodorus* (*Nanidorus*) *christiei* (Allen, 1957) Siddiqi, 1974

Morphometric data: see Table 9.

Males not found.

Discussion on morphometric characters

Females from *Quercus serrata* have stylet 33–40μm long. This measurement appears rather great for this species.[1,5,8,17,24,25] Loof[15] states that he doubted Allen's indication "stylet length 33 –47μm in *christiei*", since species of the subgenus *Nanidorus* usually have very short stylets. He remeasured stylet length of five paratypes of *christiei* out of 38, and found that they had the stylet length of 27–33μm. While Bird and Mai[3] report that the stylet length of 1,371 specimens from 22 populations ranges 30–42μm, the maximum being 140% of the minimum. These reports suggest that the stylet length of this species is much variable between populations and even within a population.

One female has the extremely assymmetrical gonads, the anterior normally developed (106μm in length) and the posterior poorly developed (42μm).

Host species and distribution

P. (*N.*) *minor* appears less abundant and restricted to central to western Japan in forest nurseries.[12,17,35] Specimens are less abundant also in Meiji Shrine Forest; the recorded host plants are *Juniperus* sp., *Rhododendron obtusum*, *Pinus densiflora* and *Quercus serrata*. The author has obtained two females from the primeval forest soil in Hachioji City, central Japan. This species appears native to Japan.

Table 10. Morphometric data on *Paratrichodorus* (*A.*) *porosus* (specimens from the root-zone of *Daphniphyllum macropodum*)
Females (n=20)

Characters	$\bar{X}$	Range	S. D.	C	max/min
L (μm)	594	464 -747	77	0.130	1.61
Neck length (μm)	127	95 -155	17	0.131	1.62
Stylet length (μm)	50.4	41.9- 58	3.8	0.075	1.38
Fore end to excretory pore (μm)	86	70 -108	9.6	0.112	1.54
Fore end to vulva (μm)	333	264 -420	41	0.123	1.59
Ant. ovary length (μm)	127	83 -256	34	0.265	3.09
Post. ovary length (μm)	123	79 -175	29	0.237	2.20
P1[a] to P2[b] (μm)	9.6	6.3- 13.8	2.2	0.234	2.19
P2 to Vulva (μm)	10.2	6.1- 15	2.4	0.240	2.46
Vulva to P3[c] (μm)	6.1	4.6- 8.7	1.2	0.192	1.89
P3 to P4[d] (μm)	11.6	7.1- 17.9	3.1	0.30	2.52
Ratios-a	17	15 - 21	1.6	0.096	1.47
-b	4.8	4.2- 5.5	0.5	0.107	1.31
-V	55.9	53.8- 58.1	1.1	0.020	1.08
-G_1	21	18 - 26	3.8	0.178	1.90
-G_2	20	15 - 28	3.0	0.150	1.81
-Fore end to excretory pore/Neck length (%)	68	57 - 80	8	0.118	1.41

[a,b,c,d] Ventromedian advulvar pores numbered from the foremost.

Table 11. Variation in the number of ventromedian pores in females of *Paratrichodorus* (*A.*) *porosus*

Host species[a]	Number of ventromedian pores		
	n	4	3
Ginkgo biloba	17	17	
Taxus cuspidata	8	8	
Pinus thunbergii	1	1	
P. densiflora	5	4	1
P. pentaphylla	3	3	
Juniperus sp.	3	3	
Carpinus tschonoskii	4	4	
Quercus acutissima	3	3	
Q. serrata	3	3	
Q. salicina	4	4	
Castanea crenata	2		2
Castanopsis cuspidata	5	5	
Celtis sinensis	2	2	
Aphananthe aspera	2	1	1
Cercidiphyllum japonicum	11	9	2
Magnolia obovata	6	6	
Cinnamomum camphora	1	1	
Neolitsea sericea	1	1	
Daphniphyllum macropodum	25	25	
Ilex integra	2	2	
Acer palmatum	5	5	
Ternstroemia japonica	20	19	1
Cleyera japonica	18	17	1
Eurya japonica	2	2	
Idesia polycarpa	1	1	
Aucuba japonica	7	7	
Fatsia japonica	1	1	
Rhododendron indicum[b]	3	3	
Callicarpa japonica	1	1	
Viburnum awabuki	1	1	
Total	167	159	8

[a] Females not obtained from: *Rhododendron obtusum*, *Ligustrum japonicum*.
[b] In the garden of Univ. Tokyo.

Paratrichodorus (*Atlantadorus*) *porosus* (Allen, 1957) Siddiqi, 1974

(Fig. 4.D–F)

=*Trichodorus porosus* Allen, 1957

=*Trichodorus bucrius* Lordello et Zamith, 1958

Morphometric data: see Table 10.

Males not found.

Variation in the number of ventromedian advulvar pores

According to Allen,[1] *P.*(*A.*) *porosus* female is characterized by the presence of the pair of ventromedian pores anterior and posterior to the vulva. Since the original description by Allen, this species has been reported from several districts of the world.[13,16,17,19,24,28,31] Siddiqi[24] reported a female with five ventromedian pores from California. Nishizawa[19] found females without the posterior pore of the postvulval pair occurring in natural population in about 30 percent of the females. He investigated a natural and reared populations and suggested that occurrence of females lacking the last pore is determined genetically.

Females with only three ventromedian pores have been found also in several populations in Meiji Shrine Forest (Table 11). It is suggested that the variation in the number of ventromedian pores occurs in rather high frequency in natural populations and that this character is rather variable. Although Nishizawa reported females with two or five ventromedian pores from reared population, such specimens have not been found in Meiji Shrine. All the females with only three ventromedian pores among Meiji Shrine specimens lack the foremost one, while those in Nishizawa's population lack the last one.

Host species

P.(*A.*) *porosus* has been found associated with various forest trees in Meiji Shrine Forest; five species of conifers and 27 species of broad-leaved trees (Table 11), which suggests a wide host range and a wide distribution of the nematode.

The author thanks Mr. Y. Ohshima who kindly commented on the manuscript and made a suggestion on nomenclature for a new species; Dr. M. Ichinohe and Dr. A. Gotoh who commented on the manuscript; and Prof. Dr. A. Coomans, Dr. E. Geraert and Dr. W. Decraemer who instructed him by letter.

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和文摘要

樹木に寄生する線虫類の分類学的研究
1. Trichodoridae 科

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樹木と土壌線虫との関わりを究明するための基礎資料を得，また地域の線虫相を探る目的で，明治神宮境内林を中心に樹木の根辺土壌より得られた植物寄生性線虫類の分類学的研究を行った．本論文はその第1報で，Trichodoridae 5種の形態に関する知見を報告する．*Trichodorus tricaulatus* n. sp. は雄・雌共 *T. sparsus* Szczygiel, 1968 に近似するが，食道腺が腹側で腸に重なること，雄は ventromedian cervical pore を3つ持つこと，交接刺の striation と scale は先端を除く前半部に限られることにより区別される．*T. aequalis* Allen, 1957 は北アメリカ以外の地域から初めて報告された．*T. cedarus* Yokoo, 1964 の種内変異，Yokoo の原論文の検討から，*T. longistylus* Yokoo, 1964, *T. kurumeensis* Yokoo, 1966 は *T. cedarus* の junior synonym とされた．*Paratrichodorus* (*Nanidorus*) *minor* (Colbran, 1956) は日本に土着の種と見られる．*P.*(*Atlantadorus*)*porosus*(Allen,1957) は，調査地域内に於て広い寄主範囲を示した．*P.*(*A.*) *porosus* の ventromedian pore の数の変異は，自然集団に於てかなり高い頻度で見られるものと思われる．以上5種の形態計測値を記載し，*Trichodorus* 3種については種内変異に言及し，若干の論議を行った．